D. PROJECT DESCRIPTION

D. 1. Results of previous research

J. Runge is PI on two relevant NSF awards, (*US-GLOBEC NEP Phase IIIa: Efffects of Climate Variability on Calanus Dormancy Patterns and Population Dynamics within the California Current*: OCE- 0733881; $156,199; 03/19/2005-05/31/2008 and *U.S.-GLOBEC: NWA Georges Bank: Effects of climate variability on Calanus dormancy patterns and population dynamics in the Northwest Atlantic*: OCE-0733910; $182,013; 11/01/2005-10/31/2008) in which A. Leising was collaborator and C. Johnson was supported in part as postdoctoral research associate. These projects were part of previous phases supporting synthesis of U.S. GLOBEC Northeast Pacific and Georges Bank/Northwest Atlantic program data. We compiled data sets from both regions and developed a life cycle model (for comparison of life cycle model to data, see Figure 1, section D.5.4) to look for common mechanisms controlling diapause in *C. finmarchicus*, *C. pacificus* and *C. marshallae* from these regions. The research resulted in elaboration of the Lipid Window Accumulation hypothesis (Johnson et al. 2008) that is described in the project description below. To date, the research has been presented at 9 national and international meetings or seminars and the award has supported preparation of 4 additional research articles (Ohman et al. submitted; Leising et al. in prep. a, b; Castonguay et al. in prep) and 2 book chapters (Harris et al. in prep; Maloney et al. in prep.). In addition to supporting C. Johnson as a postdoctoral researcher, the NW Atlantic award is contributing to support of a new graduate student at the University of Maine, J. Braff, who will be investigating lipid accumulation in species of *Calanus* with laboratory experiments at the Darling Marine Center.

A. Pershing is Co-PI on *US-GLOBEC: NWA/Georges Bank - Marine Ecosystem Responses to Climate-Associated Remote Forcing from the Labrador Sea* (OCE-0625273; $251,420, 05/01/06-04/31/08). This project continues to synthesize the response of the Gulf of Maine to climate variability and change. It led to a recent publication in *Science* on impacts of change in the Arctic on northwest Atlantic shelf ecosystems (Greene and Pershing, 2007).

D.Kimmel is Senior Investigator on *OCE-0453905, Dynamic Stability and Particle Transformations: Tracing Pathways of Production in Estuarine Turbidity Maxima (*$413,587, Kimmel budget only;10/2005 – 9/2009, PIs: E. D. Houde and others). The goal of this NSF project is to examine trophic interactions in the estuarine turbidity maximum (ETM) of Chesapeake Bay, which acts as an aggregation zonefor zooplankton and fish, thus are critical nursery areas for anadromous fish. A combined laboratory, field and numerical modeling approach investigates trophic transfer in the ETM. To date, there have been over 20 presentations and 6 publications associated with this award.

D.2. Introduction

Planktonic copepods in the genus *Calanus* are prominent in the basins and deep coastal areas of the temperate, subarctic and polar oceans. Here we focus on two species pairs that are numerically and biomass dominant in temperate and subarctic shelf waters of North America. The dominance of *C. finmarchicus* in the zooplankton assemblage of the subarctic N. Atlantic has motivated extensive research on this species by the U.S., Canadian and European oceanographic communities. The prominence of *C. helgolandicus,* the warm-temperate congener of *C. finmarchicus* (Fleminger and Hulsemann 1977) in the North Sea and eastern boundary current off Europe and North Africa has prompted numerous studies by European investigators. In the North Pacific Ocean, *C. marshallae* is a common boreal shelf copepod with a geographical distribution concentrated in waters off of the Gulf of Alaska, Aleutian Islands and in the eastern Bering Sea. Its warm-temperate counterpart, *C. pacificus* (Frost 1974), is prominent in Puget Sound and the California Current system.

These sympatric species pairs (*C. marshallae* and *C. pacificus* in the Northeast Pacific; *C. finmarchicus* and *C. helgolandicus* in the North Atlantic) comprise two analogous, congeneric sibling groups (Frost 1974; Bucklin et al. 1995): the “helgolandicus” group, including *C. helgolandicus* and *C. pacificus* and the “finmarchicus” group, including *C. finmarchicus* and *C. marshallae.* As we report in the background section below, knowledge of the population dynamics and physiological processes controlling life histories of these species has been accumulating over the past 15 years, supported in large part by studies within the U.S. and International GLOBEC programs.

We propose a synthesis that will compare and contrast the life histories of the two species pairs and make predictions about how they will respond to climate change. We will identify common processes controlling recruitment and population dynamics among the species and establish a set of parameters that describe the physiological rate responses particular to each species, to the best of our current knowledge. We intend to describe the life histories of each of the four species with a general life cycle model that adequately represents seasonal patterns in life cycles across species and ranges. We will then use this model to predict how the different species would respond to reasonable scenarios of climate change in the respective oceans. We will identify critical data needs for observing and predicting change in *Calanus* species across their ranges and for developing measurement metrics that characterize the role of *Calanus* in temperate and subarctic marine ecosystems. We will also synthesize mortality measurements and test new approaches for estimating copepod mortality rates needed to constrain the model.

Our proposed research falls under the population dynamics and recruitment of target species theme. It addresses the specific U.S. GLOBEC goals to: (1) understand the potential impacts of climate variability and change on the dynamics of shelf ecosystems and on the distribution, abundance and production of several specific target species; (2) embody this understanding in conceptual and quantitative models capable of capturing population and ecosystem responses over a broad range of spatial and temporal scales; and (3) improve predictions of U.S. living marine resource populations which can lead to enhanced management capabilities (see our significance and broader impacts section).

A key conceptual cornerstone to our approach is the understanding of diapause (we will use the term dormancy). In a prior U. S. GLOBEC synthesis grant, we developed the Lipid Accumulation Window Hypothesis (LAW) to explain dormancy patterns of *C. finmarchicus* in coastal waters of the Northwest Atlantic Ocean (Johnson et al. 2008). According to this hypothesis, individual *Calanus* can only enter diapause if their food and temperature history allows them to accumulate sufficient lipid for overwintering, molting and early gonad development. We hypothesize that timing of entry and exit from dormancy, as modulated by species-specific physiology and effects of climate-forced variability of food and temperature on lipid accumulation, exerts a critical biological control on *Calanus* population dynamics.

We will test the generality of the LAW hypothesis across species and ranges using an individual-based *Calanus* life cycle model (Johnson et al. 2007; Leising et al. in prep.) with species-specific parameters representing differences in the processes controlling growth, recruitment and other life history characteristics. Our 1-D modeling approach will focus on life history responses to climate change scenarios involving changes in temperature, food and mortality regimes. We argue here that in many regions, life history responses to seasonal cycles of food and temperature determine the local productivity of *Calanus* species.

We recognize, nevertheless, that climate forcing on circulation and consequently transport of *Calanus* between regions and from deep water to coastal shelves is also important, perhaps crucially. We have elected to employ a 1D approach to facilitate development of the model. Although this approach will not capture changes to advective fields, it will provide a detailed view of the influence of local processes on the population dynamics of *Calanus*.To address whether climate forced variability in large scale advection will affect *Calanus* species distribution and abundance, we will seek collaboration either within the U.S. pan-regional synthesis PI community, once it is selected, or in the broader research community, to link our life cycle model with coupled physical-biological models.

We will undertake this research with a core group of university PIs and extensive collaboration from NOAA, Canadian and European colleagues. A. Leising (NOAA) and C. Johnson (Canada DFO) are primary contributors to the prior GLOBEC dormancy project. D. Mackas (DFO Canada) has been helpful in providing access to his zooplankton data sets. S. Plourde (Canada DFO) will collaborate with J. Runge and postdoctoral associate J.J. Pierson, who has extensive experience with the Pacific *Calanus* species, in the compilation and analysis of *Calanus* recruitment and demographic data. Our modeling experience includes A. Leising, who developed the original *Calanus* life cycle model, A. Pershing, who is currently involved in development of a coupled physical biological model for predicting of *Calanus* abundance and distribution as prey for right whales in the Gulf of Maine, and postdoctoral research associate, F. Maps, who will complete in 2008 his Ph.D. research on coupled physical biological modeling of *C. finmarchicus* in the Gulf of St. Lawrence. With experience in developing regional climatologies, D. Kimmel will contribute to the elaboration of climate scenarios. In addition to collaboration with PI's of other pan-regional synthesis projects, we will seek opportunities to engage with our European colleagues, including R. Harris (UK), A. Gislason (Iceland) and D. Bonnet (France), for collaboration on the life history dynamics of *C. finmarchicus/C. helgolandicus* in the northeast Atlantic and North Atlantic basin.

D.3. Background

D.3.1. Biogeography of Calanus

C. finmarchicus is found across the north Atlantic from approximately 40°N- 70°N, including both open-ocean and coastal regions (Barnard et al. 2004). The distribution of *C. helgolandicus* overlaps *C. finmarchicus* on the southern edge its range in the northeast Atlantic, and extends to 30°N in the central N. Atlantic. Each species has different centers of maximum abundance. *C. finmarchicus* is most abundant in the Labrador Sea and off Norway and *C. helgolandicus* is concentrated in the waters around the British Isles and in the Mediterranean Sea, particularly in the Adriatic (Bonnet et al. 2005). The overall distributions of both species have shifted northward over the last 50 years (Bonnet et al. 2005), and there is evidence of a long-term decline in *C. finmarchicus* in the northeast Atlantic (Fromentin and Planque 1996).

Less information is available on *Calanus* basin-scale distribution in the Pacific. *C. marshallae* (in the "finmarchicus" group) is found in the Bering Sea and coastal Northeast Pacific, including the upwelling zone off Oregon and Washington (Lamb and Peterson 2005; Morgan et al. 2003), over the shelf in the Gulf of Alaska (Incze et al. 1997), and in Puget Sound (Osgood and Frost 1994). The distribution of the more temperate-adapted *C. pacificus* overlaps with *C. marshallae* in the coastal Northeast Pacific, north of 40°N, but *C. pacificus* is also found south to the tip of the Baja Peninsula and west throughout the Pacific and into the Sea of Japan. In general it resides offshore of *C. marshallae* where the two overlap, and in warmer water.

Both *C. finmarchicus* and *C. pacificus* have been divided into ostensibly allopatric subspecies, based on genetic or morphological characteristics (Brodsky 1965; Bucklin et al. 1995;1996;2000). Bucklin et al. (1996) found significant frequency differences in 16S rRNA sequences in *C. finmarchicus* between the Northwest Atlantic and the Norwegian Sea suggesting that there may be distinct populations inhabiting regions with different annual cycles. Based on the known distributions, GLOBEC projects in the Northeast Pacific encountered both *C. p. oceanicus* and *C. p. californicus* in the Gulf of Alaska and CCS regions, respectively. These results leave open the possibility of phenotypic differences in life history responses within species across regions.

D.3.2. Life cycle variability

In general, the life cycles of our target *Calanus* species are multigenerational, *i.e.* there are several generations per year punctuated by an overwintering, dormant phase typically in preadult fifth copepodite stage (CV) (Conover 1988). CVs enter dormancy in late summer and fall, carrying with them large (relative to body weight) lipid stores that sustain metabolism during overwintering, molting and development of gonads (Rey Rassat 2002a). Dormant CVs are characterized by residence in deep water, reduced metabolism and arrested or slowed development In mid-late winter (typically), CVs leave dormancy, molt into adults, and mate. Females then reproduce in response to food levels, for which chlorophyll *a* concentrations are a useful proxy (Runge et al. 2005). In polar *Calanus* such as *C. hyperboreus*, internal body stores including lipids are used to produce eggs without an external food supply (Conover 1988). However, the extent to which internal body stores contribute to egg production in the "finmarchicus' group is still unresolved.

There is considerable variability in the timing of dormancy and the numbers of generations across regions and species of *Calanus* (e.g. Planque et al. 1997; Hind et al. 2000; Johnson et al. 2007; Bonnet et al. 2005; Osgood and Frost 1994). For example, *C. finmarchicus* in the coastal Gulf of Maine emerges from dormancy in late December in the Gulf of Maine (Durbin et al. 1997) and produces 2-3 generations over the course of a season. In contrast, in the adjacent slope water, exit from dormancy is 2-3 months later and only one generation is produced. *C. marshallae* exhibits similar variability in the number of generations between Puget Sound and the Oregon upwelling zone (Osgood and Frost 1994; Peterson 1998). In many populations, not all stage CV enter dormancy; some continue to molt on to adults and reproduce (e.g. Durbin et al. 1997; Heath et al. 2008; Kobari et al. 2004; Ohman et al. 1996).

We hypothesize that the physiological responses of each species to variability in food supply and ambient temperature play a primary role in determining its distribution and abundance. Since climate change will influence temperature and food supply through bottom up processes, the implication is that abundance and distribution of the two species pairs will shift, depending on the magnitude of the change. The influence of climate change is not only on reproductive rate, but also on the number of generations and timing of active and overwintering periods, which are controlled by the processes determining entry into and exit from dormancy.

D.3.3. Dormancy

Understanding what controls the timing of the dormancy period is a major challenge for modeling copepod population dynamics (e.g. Runge et al. 2005). Of the hypotheses put forward to explain what causes a developing copepodid stage to enter into and then emerge from a dormant state (reviewed in detail by, among others, Hirche 1996 and Johnson et al. 2008), Johnson et al. (2008) concluded that only one, the lipid accumulation window hypothesis, was consistent with observations of variable timing of entry and exit from dormancy at four monitoring stations in different regions of the northwest Atlantic. The fundamental premise of the hypothesis is that developing copepodid individuals will only initiate hormonal/physiological processes to prepare for dormancy if their lipid stores are above a certain threshold level assuring sufficient lipids to endure overwintering, molting and early gonad development. If this lipid level is not attained, the individual develops to the adult stage. Under the hypothesis, duration of the dormancy period is also variable, dependent on ambient temperature and the level of lipid stores. As temperature and food supply are the primary exogenous factors controlling lipid accumulation; this is a potentially important mechanism by which climate change may influence copepod population dynamics. For *Calanus finmarchicus*, low ambient temperature and high food abundance yield optimum lipid accumulation.

D.3.3. Reproduction: relationships to food and temperature

Climate forcing through bottom-up influence on ambient temperature and food supply can also directly impact rates of reproduction and recruitment. The measurement and understanding of factors determining variability of copepod egg production rates, in particular for *Calanus* species, increased enormously during the GLOBEC years (e.g. Table 1).

In the northwest Atlantic in spring and early summer, the egg production rates of *C. finmarchicus* follow a hyperbolic relationship to chlorophyll *a*, but with a critical concentration corresponding to an average chlorophyll concentration of 1.6-1.8 $\mu g\ l^{-1}$ in the upper 50 m, above which food is generally not limiting to egg production (e.g. Campbell and Head 2000; Runge et al. 2006). This is considerably lower than the critical concentration indicated by general equations derived from analysis of all broadcast spawning species (Bunker and Hirst 2004), although both studies corroborated that ambient temperature has only a secondary effect. In stratified summer waters, the relationship to chlorophyll *a* breaks down (e.g. Runge and Plourde 1996; Jonasdottir et al. 2005), suggesting different trophic connections to microzooplankton (e.g. Ohman and Runge 1994).

In the northeast Atlantic, there is high variability in the relationship of *C. finmarchicus* egg production to chlorophyll, even in spring and early summer (e.g. Gislason 2005; Jonasdottir et al. 2005). Two possible explanations for this difference from the northwest Atlantic are 1) different

Species & Location	**Reference**	**Species & Location**	**Reference**
Calanus spp.		*Calanus finmarchicus* (cont.)	
NE Atlantic	Harris et al 2000	mesocosm	Nejstgaard et al. 1997
Calanus finmarchicus			Nejstgaard et al. 2001
Barents Sea	Melle and Skjoldal 1998	*Calanus helgolandicus*	
English Channel	Rey-Rassat et al. 2002a	English Channel	Hirst et al 2007
Disco Bay	Madsen et al. 2001		
Faroe shelf	Debes and Eliasen		Irigoien et al. 2000a
Gulf of St Lawrence	Ohman and Runge 1994		Irigoien et al. 2000b
	Plourde and Runge 1993		Pond et al 2006
	Plourde et al. 2001		Rey-Rassat et al. 2004
	Starr et al. 1999		Rey-Rassat et al. 2002a
Icelandic shelf	Gislason 2005		Rey-Rassat et al. 2002b
	Gislason and Astthorsson 2000	NE Atlantic	Biegala et al 1999
Irminger Sea	Mayor et al. 2006		Bonnet et al 2005
	Gislason et al. 2007		
	Heath et al. 2008		
NE Atlantic	Biegala et al 1999	North sea	Jonasdottir et al 2005
	Hirche et al 1997		Kang and Poulet 2000
	Koski 2007	*Calanus marshallae*	
	Richardson et al. 1999	Oregon upwelling	Peterson et al 2002
North sea	Jonasdottir et al 2005		Gomez Gutierrez & Peterson 1999
Norwegian Sea	Niehoff 2000	Bering Sea	Baier and Napp 2003
	Niehoff et al 1999	Chukchi/ Beaufort Seas	Plourde et al 2005
	Pasternak et al 2004	*Calanus pacificus*	
	Stenevik et al. 2007		
NW Atlantic	Cabal et al 1997	Oregon upwelling	Gomez Gutierrez & Peterson 1999
	Campbell and Head 2000		Peterson et al 2002
	Runge and Plourde 1996		Uye 1996
NW Atlantic/Georges Bank	Runge et al. 2006	Puget Sound/Dabob Bay	Runge 1984
NW Atlantic/GoM	Campbell et al. 2001b		Frost 1985
	Durbin et al 1997		Pierson et al 2005
	Durbin et al 2003	California Current	Ohman et al 1998
SW Iceland	Jonasdottir et al 2002		Mullin 1991
	Helland et al. 2003		
	Hirche 1996		

Table 1. Studies of egg production rate of the two *Calanus* species pairs

microzooplankton/autotroph prey relationships in spring and 2) phenotypic variation in the ability of *C. finmarchicus* to use lipid stores for egg production: food availability is sufficient to explain egg production rates in the northwest Atlantic (e.g. Durbin et al. 2003; Ohman and Runge 1994), but external food supply from both phytoplankton and microzooplankton appear insufficient to sustain egg production in the Irminger Sea and northeast Atlantic (e.g. Richardson et al. 1999; Mayor et al. 2006).

A hyperbolic relationship with chlorophyll *a* concentration is also reported for *C. helgolandicus* (Bonnet et al. 2005), with a critical concentration of approx. 2 µg l^{-1}, similar to *C. finmarchicus*. The maximum egg production rate (20 eggs $female^{-1}d^{-1}$) is about half the maximum rate of *C. finmarchicus* (e.g Jonasdottir et al. 2005); however, this comparison also must consider possible differences in female body size.

Reproductive strategies and output differ between *Calanus marshallae* and *C. pacificus* throughout their ranges, even in regions where the two are co-located. *In situ* observations of *C. marshallae* have shown that reproduction begins prior to the onset of the spring bloom in many locations; the females must rely on either alternate prey or on their lipid reserves, stored before entering dormancy (Baier and Napp 2003; Smith and Vidal 1984). In the Oregon upwelling zone egg production rate is related to phytoplankton concentration (Gomez-Gutierrez and Peterson 1999; Peterson 1988). In contrast to *C. marshallae*, egg production of *C. pacificus* is usually tightly coupled to food availability in both lab and field observations (Pierson et al. 2005; Runge 1980; Runge 1981), and there is very little evidence of *C. pacificus* reproducing in the absence of food. This is a trait shared by its sibling, *C. helgolandicus* (Bonnet et al. 2005), in the North Atlantic. Observations of maximum egg production rates are higher for *C. pacificus* than for *C. marshallae* (Gomez-Gutierrez and Peterson 1999 and references therein), in contrast to *C. finmarchicus* /*C. helgolandicus*. A comparative synthesis and analysis of the egg production rate data among the four species is warranted.

D.3.4. Mortality

Mortality is dynamic and difficult to quantify. Zooplankton models typically use mortality rates as free parameters that are adjusted to fit available abundance data. The extensive field studies conducted in large part with GLOBEC support made it possible to make direct population measurements that could be used to estimate *Calanus* mortality by various methods (Aksnes et al. 1997). Stage-specific mortality estimates for *C. finmarchicus* populations at locations across the North Atlantic are summarized by Ohman et al. (2004). There was no single mortality pattern across all sites, and the not surprising implication is that the predator field in each region must be taken into account. However, there are some potentially important generalities, for example, mortality rates were highest in the earliest life stages (egg-N2) and there is evidence for density dependence with older *Calanus* stages, suggesting cannibalism as an important source of mortality. A pattern of stage-specific mortality similar to the observations on Georges Bank was also observed in the *C. finmarchicus* population in the Irminger Sea (Heath et al. 2008), and high early stage mortality was found in the *C. helgolandicus* population in the English Channel.

As an alternative indirect method for mortality estimation, Ohman et al. (2004) cite an evolutionary approach (Myers and Runge 1983) that would take into account seasonal changes in mortality over the broad region defining a subpopulation. The method provides predictions of seasonal mortality rates assuming the observed life history (notably adult body size and the development time-temperature relationship) is evolutionarily stable. The approach accurately predicted seasonal variation in mortality rates of *Acartia* clause in Jakle's lagoon, but has not been tried for other copepod populations.

D.3.5. Climate and Calanus

Most of the climate-*Calanus* relationships have been found in the North Atlantic, where there is a long-term (>40 y) data record from the Continuous Plankton Recorder (CPR; see Jossi 2003). Fromentin and Planque (1996), showed that long term changes in *C. finmarchicus* abundance in the northeast Atlantic were negatively correlated with the North Atlantic Oscillation (NAO), a regional climate index consisting of variations in pressure of the Icelandic Low and the Azores High (Hurrell 1995). Planque and

Taylor (1998) further extended these analyses by using the position of the Gulf Stream north wall, as well as the NAO, to predict *C. finmarchicus* abundance. In the northwest Atlantic, the association between C. finmarchicus and the NAO is weaker and involves a lag of 2-3 years (Greene and Pershing 2000).

The response of *C. finmarchicus* to the NAO is complex, and both in situ changes in conditions (e.g. temperature and chlorophyll) and changes in advective supply have been proposed as mechanisms. Temperature and winds have generally accepted as the two most important factors influencing *C. finmarchicus* dynamics (Sundby 2000; Beaugrand 2003). Local biological responses to seasonal cycles of food, temperature and mortality appear to control population dynamics in many regions (e.g. the Gulf of St. Lawrence: Zakardjian et al. 2003; Georges Bank: Li et al. 2006; the Central Irminger Sea: Heath et al. 2008). The abundance of outer shelf populations of *Calanus* on both sides of the Atlantic is likely sensitive to changes in the advective supply from adjacent populations (Heath et al. 1999; Pershing et al. 2004), although local conditions such as phytoplankton abundance and temperature can make up for reduced supply (MERCINA, 2003).

The climate-*C. finmarchicus* relationship in the northeast Atlantic appears to have broken down in the mid-1990s both in the northeast and northwest Atlantic (Planque and Reid 1998; Greene and Pershing 2003). Heath et al. (1999) proposed that the breakdown in the northeast Atlantic was a result of a reduction in overwintering habitat, due to a decrease in the volume of Norwegian Sea deep water. As the NAO relationship has broken down, local climate conditions are now likely driving most of the *C. finmarchicus* variability; therefore a local climatology approach is now critical to understanding *Calanus*-climate relationships. Linking local weather patterns to surface conditions will allow us to address several questions surrounding the dynamics of *Calanus* species in both basins.

The IPCC 2007 report provides several climate scenarios for future change for both the atmosphere and the ocean. The most conservative estimates suggest that air and sea-surface temperatures will likely increase at a rate of between 0.1-0.2 degrees per decade, resulting in a 1-3 degree warming by 2090. The North Atlantic is also expected to warm (Hoerling et al. 2001). Though the NAO no longer appears to impact *C. finmarchicus* dynamics, it still exerts an influence on temperature and winds. The NAO is expected to intensify (Kuzmina et al. 2005) with more frequent, positive phases (Coppola et al. 2005) and may move to the northeast (Wu and Hu 2004). The result will be warmer waters and an increase in westerly winds. Stratification of the upper ocean is likely to increase, resulting in a change in the advection of water and thus overwintering *C. finmarchicus*. This scenario will likely favor warm water species in general and the congener *C. helgolandicus* specifically (Helaouet and Beaugrand 2007). Although this warming is not likely to be equally distributed – temperature in some regions may increase more rapidly than others – it is likely that even these conservative scenarios would have a large effect on the growth patterns of planktonic organisms. For *Calanus* species, whose size, growth rate, and egg production rates are all directly affected by temperature, there should be definite impacts on its population dynamics. Long-term changes have already been observed in Atlantic and Pacific *Calanus* populations (Beaugrand (2003); Hayward 1997; Sheridan and Landry 2004; Hooff and Peterson 2006).

D.4. Objectives, based on our questions and hypotheses

The overall goal of this project is to predict the population response of *Calanus* species in the North Atlantic and North Pacific Oceans to interannual and longer term, climate-forced variability in water column temperature and food supply. Our specific objectives, addressing questions and hypotheses emerging from present knowledge and related to the overall U.S. GLOBEC goals, are outlined below. Attached to each objective are the initials of the PIs and collaborators with primary responsibility.

Table 2. Representative demographic data sets

PACIFIC

Study	**Location**	**Temporal resolution**	**Horiz. resolution**
Johnson (unpubl.)	San Diego Trough / Southern California Bight	2 wk - 3 mo / discrete months	one station / 10s – 100s km
Osgood & Checkley 1997	Santa Barbara Basin	several-month	10s km
Osgood & Frost 1994 Pierson et al. 2005 Frost (unpubl.)	Puget Sound / Dabob Bay	1 month composite / weekly – monthly / ca. 2 week	one station
US GLOBEC NEP – CCS Peterson et al.	Oregon (Newport Line)	monthly/bi-monthly	multiple stations
Mackas et al.	Western Vancouver Is.	several-month	10s km
US GLOBEC, NEP – CGOA Koyle et al.	Central Gulf of Alaska (Seward Line)	monthly/several months	10s km
Waddell & McKinnell 1995	Ocean Weather Station P	monthly/bi-monthly	one station

ATLANTIC

Study	**Location**	**Temp. resolution**	**Horiz. resolution**
PULSE Runge (unpubl.)	Gulf of Maine (Jeffrey's Ledge)	weekly	one station
GLOBEC- Georges Bank	Georges Bank	monthly	ca. 40-50 km
AZMP	Scotian Shelf / Newfoundland Shelf / Anticosti Gyre (GSL)	monthly/ bi-monthly	one station
Plourde et al. (2001, 2002, unpubl.)	Lower St. Lawrence Estuary (LSLE)	bi-monthly composite	one station / grid of 29 stations
TASC	NE Atlantic	monthly / several months	ca. 10s-100s kms
Hirst et al (2007)	English Channel	weekly	one station
Lindeque et al (2006)	Irminger Sea	several months	ca. 10s-1000s km
Gislason & Astthorsson (1996, 1998) Gislason et al. (2000, 2007) Astthorsoon & Gislason (2003)	Iceland	monthly/ bi-monthly	several stations

1. <u>Compile and analyze data sets</u> across species and regions, with the objective of publishing a series of comparative synthesis papers treating each the following subjects:
   a. <u>Demographic data across regions for each of the four *Calanus* species (JP and JR).</u> We have already compiled time series demography and indices of dormancy transitions for *C.*

finmarchicus in coastal waters of the NW Atlantic (Johnson et al. 2007) and for *C. pacificus* and *C. marshallae* in the California Current (Leising et al. in prep.). We propose to expand this analysis to other regions and data sets in the North Atlantic and North Pacific, including the Gulf of Maine, Northeast Pacific, and Northeast Atlantic (Table 2) and including *Calanus helgolandicus* in collaboration with C. Johnson, D. Bonnet, D. Mackas and others. These demographic data will be used to test the generality of our life cycle model across species and ranges.

b. Physiological rate characteristics across species and regions: egg production, growth and development rate data (JR, JP). We propose to compare and contrast egg production rate responses to food availability and temperature across regions and species to address the question: *are there common relationships among these physiological rates and food and temperature*? Our working hypothesis is that there is a common weight-specific egg production-chlorophyll *a* relationship, at least for *C. finmarchicus*, and that egg production rates at sea are relatively independent of ambient temperature. Alternatively, there may be phenotypic/ regional differences in the relationship between egg production rate and environmental variables. Similarly, we will compare growth and development rates (mostly from laboratory studies, as field data are sparse) with food availability and temperature across regions and the four species. This will be done in collaboration with S. Plourde, A. Gislason, D. Bonnet and others.

2. Develop climatologies in selected regions to test the sensitivity of life histories to climate change (DK, JP). We refer to regions identified by the locations in Table 2. Climatologies of surface mixed layer and deep temperatures, as well as chlorophyll *a* concentration will be compiled for the life cycle model. We will also develop synoptic climatologies from sea level pressure (SLP) and satellite data. We will extrapolate the climatologies into the future to represent reasonable alternative environmental states under climate change forcing. This objective will be carried out with the collaboration of C. Johnson and others.

3. Investigate mortality (AP, JR, AL). In our life cycle model, mortality rate is a closure term, guided by the empirical evidence for density dependence and high mortality in the early life stages. This objective addresses the questions: *Are there common regional and/or global patterns of mortality across species or must they be determined empirically for each species and region? Are the stage-specific, temperature-dependent mortality rates needed to accurately close life cycle models consistent with life history theory?* For each species, we will calculate "climatological mortality" based on life history theory (*sensu* Myers and Runge 1983) and observed life history characteristics. We will compare this mortality with observed mortality rates in each region, where available, and with the mortality term needed to achieve stability of the life cycle model. We will explore life history theory as an approach to investigate whether life history characteristics (functional rates of growth, development and fecundity) of each species could change sufficiently in response to different mortality and climate change scenarios.

4. Refine our stage-structured, IBM life cycle model developed for analysis of *Calanus* demography for each species (AL, FM, AP). Combined with our best understanding of fecundity and growth response parameters particular to each species, the stage-structured individual based model (IBM) (Johnson et al. 2008; Leising et al. in prep.) with species-specific parameterization represents our best integrative, quantitative understanding of *Calanus* life history dynamics. Here we address the questions: *Does the life cycle model adequately represent common processes controlling life histories within and among the two species pairs? Is the Lipid Accumulation Window hypothesis general across species and range?* We will test the model against data sets for each species from selected regional locations (e.g. Table 2), from data compiled for objectives 1 and 2 above. We will consider alternate parameterizations and diapause strategies and develop more regional or species-specific life cycle

model structures as needed, depending on evaluation of the results. We can then examine the question, *How do* Calanus *life histories and population dynamics compare between the shelf and deep ocean?* The spring and summer primary production cycles are substantially different on the shelf and in the deep ocean, and *Calanus* population dynamics and responses to climate scenarios may be fundamentally different than in the coastal ocean. This analysis will be carried out in collaboration with C. Johnson, S. Plourde and our European colleagues.

5. Using the life cycle model with parameterization tuned to each of the four species, evaluate the sensitivity of *Calanus* life history responses to the climate change scenarios developed in objective 2 (AL, FM, AP, JR). Here we will examine the null hypothesis that realistic predictions using the life cycle model and reasonable regional climatology scenarios will not substantially alter species abundance and distribution patterns against the alternative that climate change scenarios will significantly alter *Calanus* species abundance and distribution through bottom up effects of temperature and food supply on life history processes, including physiological rates and diapause responses. We will address the question: *How do the sibling species between and within the "finmarchicus" and "helgolandicus' groups respond to similar modes of climate forcing*? This analysis will provide predictions of any major shifts in distribution among the *Calanus* species. It will be carried out in collaboration with all our Canadian and European colleagues.

We will also look for opportunities to interact and leverage results from this project with other projects both within and outside the GLOBEC programs. If projects to evaluate climate forcing on circulation and temperature patterns are included in the pan-regional synthesis, we will look for opportunities to link our1-D life cycle model predictions of life history changes with 3-D circulation and temperature fields (AL, FM) to investigate the null hypothesis that changes in advection does not substantially change predictions from the 1-D life cycle models against the alternative that changes in advection, especially influencing transport of overwintering stages, has a significant impact on abundance, distribution and seasonal cycles.

D.5. Proposed Research: Approaches and methods

D.5.1. Compilation and analysis of data

D.5.1.1. Life history demographic characteristics.

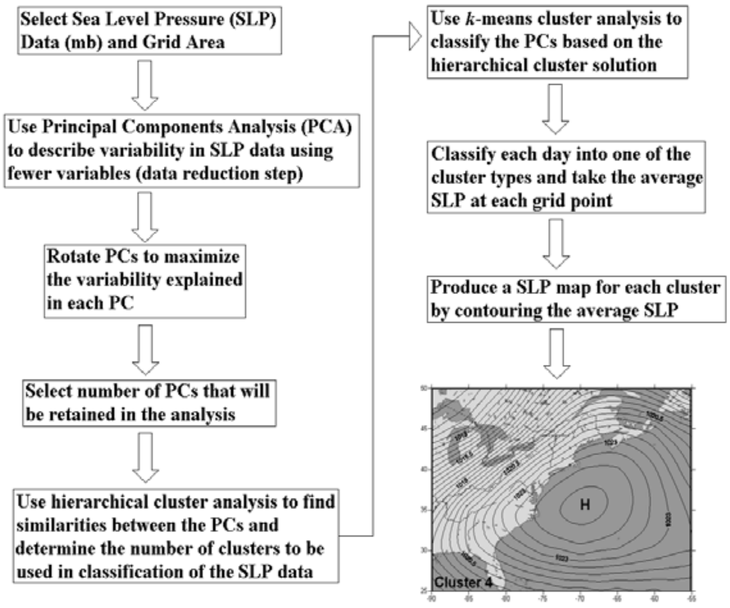
Data to be used in this study are listed in Table 2. These data will form the basis for comparisons between model results and observed data. Population metrics, including the peak abundance, timing of the abundance peak, duration of the reproductive period (defined as the time between emergence from and entry into dormancy; methods in Johnson et al. 2007), the rate of population growth between emergence and the population abundance peak, and the relative timing of emergence from dormancy and the spring bloom, will be used to compare populations at different locations. In conjunction with physiological rate data, environmental data, and the IBM, these metrics will provide used to address questions about interactions among food, temperature, egg production, and mortality during the productive spring season. For example, in some locations *Calanus* abundances rapidly increase immediately after emergence with peak abundances early in the year (Durbin and Casas 2006; Hirche et al. 2001), while in others, the population maximum of *Calanus* occurs later in the season despite high reproductive output early in the year (Irigoien and Harris 2003; Pierson et al. 2007; Plourde et al. 2001). These disparate life cycle patterns suggest that different factors are affecting the recruitment of the populations. These analyses will provide key insight into the similarities and differences between populations, both for different species and across regions. When coupled with the climatological information and climate predictions, these comparisons will allow us to make predictions about how *Calanus* species will respond to regional climate changes.

D.5.1.2. Calanus egg production rates.

Data on egg production rates for each of the four *Calanus* species are now available (Table 1). We will compare relationships of egg production rates to food availability and ambient temperature within species across regions and among species. We will analyse the data in several ways. First, we will relate egg production rate to chlorophyll a concentration (most likely as mixed layer mean) for each species and region by fitting with an Ivlev function similar to the analysis reported by Runge et al. (2006). Egg production rate (EPR) will be expressed as eggs female^{-1}d^{-1} and wherever possible also converted to mass specific rate %C d-1 using conversions for female body length or dry weight to carbon mass and for egg diameter to egg carbon mass (Kiorboe et al. 1985). The critical concentration will be estimated as 90% of the fitted maximum EPR. We will test for secondary relationship with mixed layer temperature (and other measures of food availability, where available) by analysis of residuals (e.g. Runge et al. 2006). We will also use a generalized linear model (GLM) approach, as described by Bonnet et al. (2005), in which predictors are mixed layer temperature, chlorophyll a concentration, latitude, longitude and time of year, using transformed data where needed. Non-significant terms ($p<0.05$, F test) will be removed by backward stepwise regression.

D.5.2 Development of climatologies

Synoptic climatology is a technique that has been used in physical geography for many years (Yarnal 1993). It is simply the classification of sea level pressure (SLP, *i.e.*, weather) patterns that occur over regional spatial scales (100-1000s of km). Each SLP pattern is then "down-scaled" to determine the average surface conditions that occur during the passage of each SLP pattern. The procedure is illustrated in the figure below. The result is a series of SLP patterns that are linked to surface variability. Unlike large-scale climate indices, which are differences in sea level pressure at two locations, synoptic climatology allows the quantification of climate effects in a variety of user-defined spatial regions. The use of regional weather patterns to predict a local environmental response is a powerful tool that can be used to describe a wide range of environmental forcing functions driving *Calanus* spp. dynamics.



Synoptic climatology.

Methods for classifying sea level pressure (SLP) data into weather patterns are presented in Miller et al. (2006). We will follow their methods and modify the weather classification for the Atlantic and Pacific Oceans. SLP data at 5 degree spatial resolution will be acquired from National Center for Atmospheric Research, http://www.ncar.ucar.edu). Sea level pressure data is available from 1899, but the most reliable data dates from 1950 to the present. We will create 3 local climatologies for each basin. A separate set of SLP pressure data will be analyzed for each region resulting in distinct weather patterns being classified for each region.

Downscaling to regional conditions.

Once weather patterns are classified, we will relate these patterns to surface and oceanic conditions. We will define regions around the locations and data sets selected for detailed analysis. For example, the North Atlantic may be divided into three large scale regions (Norwegian Sea, Central North Atlantic, northwest Atlantic, corresponding to the 3 semi-distinct gyre systems (Bucklin et al. 2000) and populations of *C. finmarchicus* (Planque et al. 1997). Subregions, such as the Gulf of Maine, may also be defined. Global data are available for a variety of meterological variables (e.g., air temperature, precipitation, winds) from the NCEP/NCAR Reanalysis data set (Kistler et al. 2001; http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.surface.html) at 2.5ºdegree spatial resolution. Ocean temperature and chl. *a* concentration data will be acquired from the World Ocean Database (NODC; http://www.nodc.noaa.gov/General/getdata.html), and mixed layer depth will be calculated from CTD profiles using the method described in Montegut et al. 2004.

The frequency (in days) of each weather pattern, for each region, will be determined and placed in a matrix along with monthly meteorological and oceanic conditions. We will determine the empirical relationship between weather pattern frequency and oceanic conditions using cross correlation analysis, as oceanic conditions are likely to have a lagged response to particular weather patterns. This analysis will link weather pattern variability to oceanic conditions, in particular those oceanic conditions that will be used in models of *Calanus* population dynamics, and identify key weather patterns as candidates for global change scenarios. Our established relationships between key weather patterns, oceanic conditions and *Calanus* dynamics can be used to test scenarios of global change and link our project with other pan-regional GLOBEC projects. For example, the output of a general circulation model may predict a change in SLP patterns over the north Atlantic. We can quantitatively show how this change in SLP will be related to the frequency of key weather patterns, the change in ocean conditions and the biological response of *Calanus* spp.

D.5.3 Investigation of mortality

The most comprehensive data set for mortality rate is the comparative study of C. *finmarchicus* patterns at localities across the N. Atlantic (Ohman et al. 2004). As this study indicates, finding one mortality function suitable for multiple regions, let alone multiple species, will be difficult. In a recent effort to model the basin-scale distribution of *Calanus finmarchicus*, Speirs et al. (2006) fit a stage-dependent mortality function in which mortality increases with temperature or when food (chlorophyll) falls below some threshold level. Density-dependent mortality is also included in their scheme. Their model can produce realistic *C. finmarchicus* abundance patterns across the North Atlantic. However, when the Speirs et al. (2006) formulation is employed in a model of the Gulf of Maine, the resulting mortality rates cause the population to crash (Pershing et al., submitted). By adjusting the parameters in the Speirs formulation, we were able to accurately simulate the development of the Gulf of Maine *C. finmarchicus* population.

Simulating the response of a population to novel physical conditions, *i.e.*, climate change scenarios, poses a similar challenge. We propose to use life history theory (Myers and Runge 1983) to derive seasonal and regionally specific mortality rates. The technique begins with the assumption that a population’s schedule of reproduction and growth represents an evolutionarily stable strategy, one that evolved under a specific mortality regime. We can infer this mortality regime by finding the survivorship schedule that makes the observed reproduction and growth patterns evolutionarily stable. By assuming that growth, development, and mortality are linked evolutionarily, the Myers and Runge (1983) approach effectively reduces the parameter space that must be searched. For our study, the development and reproduction schedules will be taken from the individual-based models under physical conditions representative of the target study regions. We will then use the life-history approach to infer seasonally varying, stage-resolved mortalities for each region and species. These mortality schedules can then be used to examine the response of the four target copepods to climate change. We will first use the IBMs to compute growth and reproductive rates under the climate scenarios. We will then estimate new mortality schedules, representing the conditions under which the population would be evolutionarily stable. If the new mortalities are much lower than the original values, then we would conclude that the species in question may not be viable at the region in question.

D.5.4-5.5. Life cycle model development and simulation

We will employ individual-based physiological and behavioral models of the four *Calanus* target species, expanding on our past modeling efforts. The goals of this phase are to (1) compare how our hypothesized dormancy controls for the target species affect population dynamics both within a single species across regions, and between different species inhabiting the same region; (2) determine the sensitivity of copepod population metrics (e.g. peak abundance, timing of peak, total egg production) to climate change, particularly changes in temperature as forecast by the IPCC 2007 scenarios, (3) examine how differences in mortality functions, i.e. density independent vs density dependent, seasonal versus constant, affect population dynamics when interacting with the dormancy phases, and (4) examine how total and carbon-relative lipid mass within the copepod population varies seasonally and interannually.

An individual-based modeling approach is used because each copepod may have a unique history of temperature and food exposure, which results in a more variable adult population than could be achieved through simple biomass following models. The use of an individual-based model makes it possible to track the body size of individuals, rather than total biomass of the entire population, or of a subgroup of a population. Size is a function of the temperature and food concentration conditions at which copepods have grown (Campbell et al., 2001; Durbin et al., 2000; Mullin and Brooks, 1970; Peterson, 1986; Vidal, 1980). The IBM models growth and development rates separately, as a function of temperature and food concentration for each species (*C. finmarchicus:* Campbell et al. 2001; *C. marshallae:* Peterson 1986; C. pacificus: Vidal 1980; *C. helgolandicus*: Rey-Rassat et al. 2002c; Bonnet in prep.). We will compile data on other physiological rates needed to run species-specific versions of the life cycle model.

In the model, individuals develop through 8 ‘stages,’ some of which are aggregates of developmental stages. Egg production rates for these four species, as a function of chlorophyll, have been measured both from field and laboratory experiments (see Table 1). The model includes separate specific controls for the dormancy pattern. To date, we have investigated several factors (Johnson et al. 2007), and have narrowed our focus to two specific controls on dormancy: the accumulation of sufficient lipid reserves relative to set thresholds, and an endogenous developmental timer. Dormancy is initiated when lipid levels reach a preset threshold and is terminated when lipid stores decrease below a pre-set threshold (lipid stores decrease during dormancy due to a temperature-controlled metabolic rate, which is highly reduced compared to active individuals). In the model, lipids are specifically tracked, with lipid accumulation and usage rates determined where possible from laboratory data (Saumweber 2006, Hakanson 1986). Additionally, the model includes a specific developmental endogenous timer, as we have hypothesized that this may also be critical to dormancy duration. This timer only operates during the dormancy period and will cause the copepods to exit dormancy if the timer reaches a certain stage, regardless of the internal lipid level. This model is consistent with observed demographies (Fig. 2) and

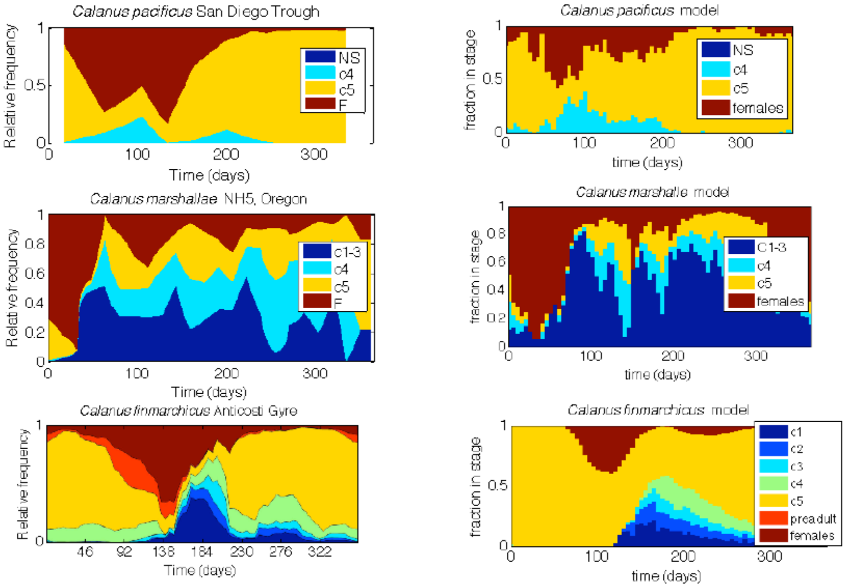


Fig. 2. Left side panels show result of observational climatologies for (top to bottom) *C.. pacificus* from the San Diego Trough, *C.alanus marshalle* from Coastal Oregon (NH5 data courtesy Bill Peterson, NOAA), and *C. finmarchicus* from the Gulf of St. Lawrence. Right hand panels show example model runs forced by climatological temperature and SeaWifs chl-a, using the LAW hypothesis for driving dormancy response. (Leising et al. unpubl.).

has to date been used successfully to make simple calculations about the sensitivities of *C. pacificus*, *C. marshallae*, and *C. finmarchicus* population dynamics to various levels of idealized physical and biological environmental change. We plan to extend our modeling to include *C. helgolandicus*, thus completing a warm/cold species pairing for comparison in the Atlantic.

We will investigate the impacts of IPCC 2007 scenarios on population dynamics using our IBMs for the four target species. Established relationships between *Calanus* spp. and local climate will be combined with global IPCC climate projections. To investigate questions about species-specific responses to similar modes of climate forcing, we will identify similar regional weather patterns and compare *Calanus* responses to these weather patterns across regions and species, through models and statistical analysis. This analysis will produce modeled projections of *Calanus* spp. abundance in different basins and will determine whether *Calanus* species respond similarly to similar types of climate variability across regions.

D.7. Management and Timeline

J. Runge will serve as project coordinator. Objectives, each achieved with one or a series of synthesis papers, have been outlined with primary responsibilities attributed to PIs and primary collaborators. There will be two annual meetings of project PIs: one in Portland, Maine and the other (not specified in activity table below) will coincide with the annual pan-regional synthesis workshop. These project meetings will have the purpose of informing and planning coordination among project components, reviewing progress and fostering new ideas and synthesis. In year 2, we have requested funding to participate in a relevant meeting or workshop in Europe (possibly associated with the Working Group in Zooplankton Ecology) attended by as many European collaborators as possible for the purpose of information exchange and coordination of collaboration activities.

Table 3. Timeline for project objectives and meetings.

Activity	**2008**	**2009**	**2010**	**2011**
Compile and analyze datasets	xxx	xxxxxxxxxxxx	xxxx	
Develop climatologies	xxx	xxxxxxxxxxxx	xxxxxxxxxxxx	
Life cycle modeling, four species	xxx	xxxxxxxxxxxx	xxxxxxxxxxxx	
Mortality investigation		xxxxxx	xxxxxxxxxxxx	xxxxxxxx
Life history responses to climate scenarios			xxxxxxxxxxxx	xxxxxxxx
Meetings				
Project PI meeting	x		x	x
Europe meeting		x		
GLOBEC PI annual meeting	(guessed) x	x	x	x

D.8. Significance and Broader Impacts

The results of this project can be applied to ecosystem-based fisheries management. Since the two *Calanus* species pairs are predominant mesozooplankton in their respective ecosystems, climate influences on their population dynamics may have a critical influence on populations of harvested fish, marine mammals and seabirds. Climate-forced changes to life-cycle timing are known to occur (Mackas et al. 1998), with impacts on recruitment in higher trophic levels (Bertram et al. 2001). Beaugrand et al.(2003) provide evidence that a change in the plankton ecosystem, including a shift from predominance of *C. finmarchicus*, whose naupliar stages are prey for larval cod, to *C. helgolandicus*, led to a mismatch in availability of copepod nauplii to larval cod and a subsequent decline in cod recruitment in the North Sea. Our synthesis will promote and identify data needs for development of a nauplius production index for use in recruitment prediction (*e.g.*, Runge et al. 1999; Castonguay et al. in prep.)

We are also developing collaborative projects at the Gulf of Maine Research Institute and with NOAA and fishing industry partners to evaluate climate change effects on lipid budgets in temperate and subarctic coastal fisheries. The role of zooplankton lipids in marine food web dynamics is increasingly recognized (*e.g.,* Kattner et al. 2007). Our research on climate change impacts on lipid accumulation in *Calanus*, a major producer of zooplankton lipids in subarctic systems, will contribute to the development and understanding of lipid dynamics in temperate and subarctic coastal fisheries, including the Gulf of Maine *Calanus*- herring-tuna interactions.

Another key outcome of this study will be an enhanced model of *Calanus* spp. growth and development, especially the dynamics of lipid accumulation and diapause. Diapausing *C. finmarchicus* are an important resource not only for both commercially important species such as herring but also for protected species such as the endangered North Atlantic right whale. With funding from NOAA and NASA, Dr. Pershing is using a stage-resolved *C. finmarchicus* model to estimate right whale feeding areas in the Gulf of Maine (Pershing et al., submitted). By incorporating a more accurate representation of *C. finmarchicus* diapause dynamics into this system, we will be able to extend our forecasts throughout the year and into important feeding areas such as the Bay of Fundy.

We will be providing training to a graduate student and two postdoctoral research associates at the interface between biological oceanography and applications to fisheries management issues, and we will be training them in a setting of international collaboration.

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